Asymmetry in Palm leaves

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(*With nine text-figures*)

The phyllotaxy of palms is always alternate. As the angular deflection between any two consecutive leaves of palms is approximately 137°, the younger of the two leaves will be nearer to the older one either by its left side or right side. This results in left-handed and right-handed palms, and the individuals of the two types of any species are generally distributed equally in any locality.

Because of this spiral mechanism arising due to the alternate arrangement of leaves, a palm leaf is always asymmetric bilaterally and the number of leaflets on one half differs from that of the other. In order to measure the degree of this asymmetry, fifteen species of which eight belonging to the pinnate type, five to the palmate type and the remaining two to a type having bipinnate leaves were selected. Among the individuals selected from these types, 54 were left-spiralled and 53 right-spiralled. The foliar spirality of the single *Nypa fruticans* palm could not be made out. The number of leaflets from the left and right halves of 453 leaves from left-spiralled palms and 457 from right-spiralled ones (excluding those of *Nypa*) were counted and the differences between halves calculated.

The pinnate palms showed a higher degree of asymmetry in the leaves. Here the left half of leaves from left-spiralled palms, and the right half of these from right-spiralled palms bore excess leaflets than their counterparts. The two species of *Caryota* bearing bipinnate leaves bore almost equal numbers of primary leaflets (rachises) on both the halves, but the ultimate leaflets in *C. mitis* showed a difference between halves. The palmate palms showed least variation between halved of leaves. Young *Rhapis excelsa*, though palmate type, behaves like a pinnate palm by showing the maximum asymmetry in the leaf.

A positive correlation exists between the number of green leaves a crown possesses and the percentage difference in the number of leaflets between halves of leaves.

Introduction

From the form of the lamina, palms may be grouped into those having pinnate or feather-like leaves as *Cocos nucifera*, palmate or fan-leaved palms as *Borassus flabellifer*, and those having bipinnate leaves as *Caryota urens*. In palm leaves, the petiole extends into the lamina region which divides the leaf blade more or less into two halves. This is not only the case with pinnate and bipinnate leaves, but also with most palmate

leaves which in fact are costa pinnate. The number of leaflets on one linear half of the leaf usually differs from the other, and this variation has a positive association with the foliar spirality of the palm. Such an asymmetry in the leaf has been studied in a number of palm species and the salient data presented in this paper.

Palm Leaves

The leaves of palms exhibit great diversity in size, shape, and division of the lamina. The largest leaf in the plant kingdom is that of a palm. Many leaves at different levels stages of maturity constitute the magnificent palm crown at the tip of the trunk, the number of green leaves in a crown varying considerably with species and individuals of the same species. The leaves are arranged spirally at the crown, the number of spirals varying with species (Davis 1970a). The foliar spiral or spirals of an individual palm either veer clockwisely or counter-clockwisely. In a species, the left-handed and right-handed individuals according to foliar spirals are distributed more or less in a 1 : 1 ratio as has been observed with the coconut (Davis 1963) and the arecanut (Davis & Kundu 1966). The foliar asymmetry in palms does not appear to be genetically inherited (Davis 1962). In very few species like *Wallichia disticha*, *Chrysalidocarpus madagascariensis*, *Neodypsis decaryi*, *Syagrus treubiana*, the leaves are not arranged spirally, instead, they fall one over another along two, three or five vertical rows (Davis 1970b).

A palm leaf may be divided into three parts—the sheath, the petiole and the blade. The lowermost part of the leaf which partially or fully surrounds the stem is the leaf-sheath. In palms like *Roystonea* sp., the sheath is tubular and elongated and appears like a continuation of the trunk, which is often spoken of as the crown-shaft. In many other species, the leaf sheath forms a beautiful mat with diagonally-moving strong fibres. The petiole represents the portion of the leaf above the sheath and having no leaflet. It is rarely round in cross-section, but mostly grooved as in *Cocos nucifera*. The margins of the petiole may be entire or provided with sharp and prominent prickles as in *Borassus flabellifer*, or beset with short and spiny leaflets as in *Phoenix sylvestris*. The leaf blade consists of the central continuation of the axis called the rachis, and the leafy tissue divided into leaflets. There are two main types of leaf blades—the palmate and the pinnate which are popularly known as 'fan-type' leaves and 'feather-type' leaves respectively. When the leaflets arise from a single point (or a narrow region) at the tip of the petiole and where the distal rachis is very much shortened, the leaf is said to be palmate. Here the leaflets, which are united at their base, are referred to as segments. The leaf of young *Borassus flabellifer* is a typical example. In *Licuala spinosa* or *Rhapis excelsa*, the clefts

between groups of fused leaflets reach up to the petiole. In the leaves of many palmate palms, a projection known as comb may be seen at the starting place of the lamina on the upper surface and/or the lower surface. In the case of pinnate leaves, the rachis is fairly long on which the leaflets are borne. The leaflets of bearing pinnate palms are free except in species such as *Areca catechu* where clusters of 2-10 leaflets remain fused. Palms like *Asterogyne martiana* with their unsplit lamina are exceptions. *Cocos nucifera* represents a typical pinnate leaved palm. Many palms described as palmate are in fact intermediaries between true palmate and pinnate types by having their rachis (or costa) only partially compressed. Such palms are said to be costa palmate, and *Livistona chinensis* forms a good example. In a few other species of palms, the leaflets or segments are further divided (pinnatisect), their ultimate divisions resembling the fin or tail of a fish in shape as in the genus *Caryota*.

Unequal halves of leaves

Palm leaves to an uncritical eye may appear to be bilaterally symmetric, one half of the lamina resembling the mirror image of the other. But on careful examination, the two halves of the leaves of most species are found to be dissimilar. This is caused presumably by the spiral arrangement of the leaves on the stem. To study the degree of this asymmetry, several leaves from 15 species of palms of which 8 belonging to the pinnate type (*Areca catechu, Chrysalidocarpus lutescens, Cocos nucifera, Nypa fruticans, Phoenix paludosa, Phoenix sylvestris, Ptychosperma macarthurii* and *Roystonea regia*), 5 to the palmate type (*Borassus flabellifer, Licuala spinosa, Livistona chinensis, Livistona rotundifolia* and *Rhapis excelsa*) and the remaining 2 to the group having branching leaflets (*Caryota mitis* and *Caryota urens*).

Individual palms ranging from six to twelve (usually half the number having right-handed, and the rest left-handed foliar spirals) from each species were selected and from each, 6-20 mature green leaves collected for making measurements and counts. However, with *Nypa fruticans*, the number of experimental palms was less than the usual number. The lengths of the lamina region as well as the longest leaflet were measured for each leaf. The numbers of leaflets (and their branches where present) on both the halves of the lamina were accounted for separately.

Presentation of Data

A. Pinnate palms

In *Areca catechu, Chrysalidocarpus lutescens, Phoenix paludosa, Ptychosperma macarthurii* and *Roystonea regia*, regular leaf spirals as seen in the coconut or *Borassus* are difficult to be traced out. But palm

leaves are always alternate, and as they are not distichous as in grasses or some scitaminaceous species, one can detect a spiral mechanism in the arrangement. *Nypa fruticans* is very odd as the leaves are always vertical arising from the horizontal rhizome. The spiralling may be clockwise or counter-clockwise. To determine the direction of the spiral, it is enough if the positions of any two consecutive leaves on the trunk are examined. If the younger leaf lies nearer the older one along the right-hand side of an observer looking from the mid-position of the older leaf, then the spirality of the palm is regarded as right-handed. If nearer by the left hand, it is considered as having a left-handed foliar spiral (Davis & Kundu 1966). In all cases, the ventral (lower) surface of the leaf has been considered for observation and accordingly, the left and right halves of the leaves refer to those halves when viewed from below, and the leaf held vertically. It may be mentioned that in species like *Borassus flabellifer*, *Cocos nucifera*, *Phoenix sylvestris*, clear foliar spirals numbering 3, 5 and 8 respectively are discernible. But in order to maintain uniformity in the data and their interpretation, palms are considered to have a single foliar spiral (based on the positions of two consecutive leaves) running clockwisely or counter-clockwisely.

1. **Areca catechu** Linn.

Table 1 shows data on the number of leaflets on halves of leaves of the two kinds of *Areca catechu* palms. In a left-spiralled palm, there is an excess of leaflets on the left half, and also the right half bears more leaflets in a right-spiralled palm. Dorsal views of leaves from a left-spiralled and a right-spiralled areca palms seen are in Fig. 1.

TABLE 1

Areca catechu: NO. OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT-HANDED PALMS

Palm	Spiral	No. of leaves	Leaflets on halves		Total	Variance of (L-R)	% difference
			Left	Right			
1	L	7	446	407	853		
2	L	8	576	537	1113		
3	L	8	469	450	919		
Total		23	1491	1394	2885	3·279	06·96
Mean per leaf			64·83	60·61	125·43		
4	R	8	471	490	961		
5	R	8	491	529	1020		
6	R	8	507	547	1054		
Total		24	1469	1566	3035	4·040	06·60
Mean per leaf			61·21	65·25	126·46		

In all the 23 leaves from the left-spiralled palms, the left-half bore excess leaflets, the excess in a leaf ranging from 1 to 9. Variance was calculated to compare the degree of variation the difference in the number of leaflets between halves of leaves from left-spiralled and

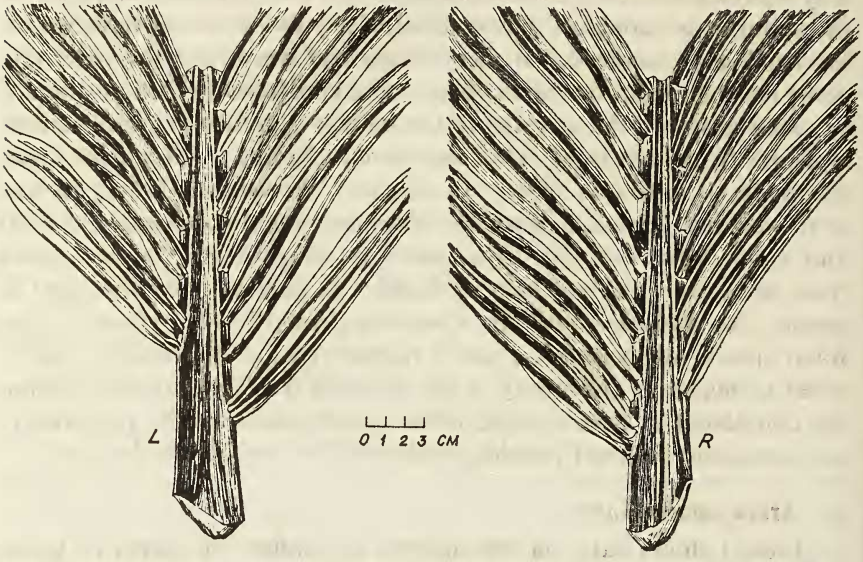

FIG. 1. Dorsal view of portions of leaves from left- and right- spiralled *Areca catechu*.

right-spiralled palms make. For the left-spiralled palms, the variance was 3·279. Tree No. 3 had the least difference in the number of leaflets between halves. The percentage excess of leaflets on the left-half over the right as given in Table 1 is 6·96. In the 24 leaves from the right-spiralled palms, the right half bore more leaflets and the difference for the different leaves ranged from 1 to 9. Tree 4 showed the least variation. The percentage excess of leaflets on the right half over the left is 6.60 which is slightly smaller than the corresponding figure for the left-spiralled palms. All the six palms examined were 15 years old. On an average, a leaf of the left-spiralled palm bore 125·43 leaflets, and a right-spiralled palm bore 126·46, and the difference is only 0·82 per cent. Even in adult *Areca catechu* palms, many leaflets remain fused, and sometimes up to ten leaflets were found to be united along their margins. This peculiarity was exhibited in all the six palms. Only 26·79 per cent of the leaflets in these palms were free like those of an adult coconut palm.

2. **Chrysalidocarpus lutescens** H. Wendl.

Chrysalidocarpus lutescens is a suckering ornamental palm, one clump possessing even as many as one hundred shoots. Six clumps were marked at the premises of the Indian Statistical Institute, Calcutta, each bearing

20-40 suckers. The different suckers of a clump usually are of different ages and heights. Some shoots in a clump are right-handed, and others left-handed. From each clump, two almost similar shoots in stature, but one with left-handed and the other right-handed foliar spirals were selected, and six to eight leaves from each shoot lopped for recording observations on them. Data collected on these 12 shoots are presented in Table 2.

TABLE 2

Chrysalidocarpus lutescens: NO. OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- HANDED PALMS

Clump	Shoot	Spiral	No. of Leaves	Leaflets on halves		Total	Variance of (L-R)	% difference
				Left	Right			
I	1	L	8	275	258	533		
II	1	L	7	320	309	629		
III	1	L	7	285	263	548		
IV	1	L	6	294	266	560		
V	1	L	7	275	268	543		
VI	1	L	7	291	283	574		
Total	6		42	1740	1647	3387	3·713	05·65
Mean per leaf				41·43	39·21	80·64		
I	2	R	8	353	377	730		
II	2	R	7	299	313	612		
III	2	R	8	339	366	705		
IV	2	R	7	321	360	681		
V	2	R	8	285	290	575		
VI	2	R	8	317	331	648		
Total	6		46	1914	2037	3951	4·959	06·43
Mean per leaf				41·61	44·28	85·89		

Of the 42 leaves from the six left-spiralled shoots, 4 leaves had equal numbers of leaflets on both the halves and in 3 others, the right half had more leaflets. In the remaining leaves, the left half had excess leaflets and the difference per leaf ranged from 1-6. On the whole, the leaflets on the left half were in excess of the right half, and the percentage difference was 5·65.

Of the 46 leaves from the six right-spiralled shoots, the leaflets on both the halves in one were equal in number and in three others, the left half had more leaflets than the right. It may be mentioned that all these abnormal leaves were from only one shoot (No. V). For the remaining

leaves, the right half had excess leaflets compared to their counterparts ; the excess per leaf ranging from 1-10. On the aggregate, a leaf of a right-spiralled palm bore 6·43 per cent more leaflets than the left half.

On an average, a leaf of a mature shoot of *Chrysalidocarpus lutescens* possess 83·26 leaflets. There is a tendency for the lowest two leaflets on each half to remain fused. Also the topmost two leaflets on each half are united. The chance of the lowest two leaflets fusing with each other is twice as large as those at the apex. The frequency of fusion seems to be the same for leaflets on both the halves of leaves of the two types of shoots. In this respect, *Chrysalidocarpus lutescens* is more remotely connected to *Areca catechu* than *Ptychosperma macarthurii*.

3. **Cocos nucifera** Linn.

Cocos nucifera is normally a single-stemmed palm although exceptional cases of suckering and branching have been reported. The large crown possesses about 25 fully opened leaves at a time and several others in an unopened condition.

12 mature leaves each from three left-spiralled palms and a similar number each from three right-spiralled palms were harvested and measurements and counts were made on them. The data are presented in Table 3.

TABLE 3

Cocos nucifera : NUMBER OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED PALMS

Palm	Spiral	Number of leaves	Leaflets on halves			Variance % of (L-R)	differ-ence
			Left	Right	Total		
1	L	12	1213	1193	2406		
2	L	12	1276	1243	2519		
3	L	12	1166	1151	2317		
Total		36	3655	3587	7242	3·543	1·90
Mean per leaf			101·53	99·64	201·17		
4	R	12	1300	1293	2593		
5	R	12	1194	1237	2431		
6	R	12	1170	1183	2353		
Total		36	3664	3713	7377	6·092	1·34
Mean per leaf			101·78	103·14	204·92		

Of the 36 leaves from the left-spiralled palms, 8 leaves had equal numbers of leaflets on both the halves and in one, the right half had two leaflets in excess of the left. In the remaining leaves, the extra number per leaf ranged from 1-8. On an average, a leaf of a left-spiralled palm bore only 1·90 per cent leaflets more than that on the right half. All the left-spiralled palms produced on an average more leaflets on the left half.

Of the 36 leaves of the right-spiralled coconuts, 5 had equal numbers of leaflets on both the halves and in 8 leaves, the left half had excess leaflets. It may be pointed out that palm No. 4 had most of the 'aberrant' leaves (9) while palm No. 5 had none. Accordingly, palm No. 4 produced on an aggregate more leaflets on the left half. In the remaining two right-spiralled palms, the right half had more leaflets. These palms, in spite of an 'abnormal' individual, produced 1·34 per cent leaflets more on their right half over those on the left.

All the six experimental palms were adults of about 45 years old. A leaf on an average produced 203·04 leaflets. In none of the leaves was any fusion of leaflets noticed.

4. **Nypa fruticans** Wurmb.

Nypa fruticans is a prostrate, aesturial, gregarious palm with a stout branching root-stock. The green leaves, which are produced alternately one on either side of the horizontal rhizome, are erect, and this vertical posture is maintained till their drying away. In India, the natural home of *Nypa fruticans* is the Sundarbans wet forest commencing from 150 km. south of Calcutta and extending up to the shores of the Bay of Bengal. During my brief visit to the Sundarbans I could make detailed observations on the leaves of only one clump which data are presented in Table 4.

TABLE 4

Nypa fruticans : DATA ON LEAVES

Palm	No. of leaves	No. of leaflets on halves		Length of lamina
		Left	ht	
1	10	44.3	44.7	3 metres

N.B.—It was difficult to determine the spirality of this palm (shoot).

Although the data are very limited, one gets the impression that the leaves are more or less bilaterally symmetric so far as the number of leaflets are concerned.

5. **Phoenix paludosa** Roxb.

This species is also found flourishing in the Sundarbans in a wild condition. There are a few dense clumps of *Phoenix paludosa* at the Indian Botanic Garden, Calcutta, and observations were made on some of them. Unlike the species described earlier which are androgynous, *P. paludosa* as well as the next one (*P. sylvestris*) are dioecious. *P. sylvestris* is single-stemmed while *P. paludosa* is a suckering species.

Six shoots (3 left-spiralled and 3 right-spiralled) were selected from two clumps of which one is female and the other male, and 10 fully developed green leaves were harvested from each of them for recording observations. The data are presented in Table 5.

TABLE 5

Phoenix paludosa : NUMBER OF LEAFLETS BETWEEN HALVES OF LEAVES

Spirality of palm	No. of leaves	Mean length of whole leaf	No. leaflets on L. half/ leaf	No. leaflets on R. half/ leaf	Difference	Percentage
1 L	10	90·85	30·4	29·9	0·5	1·67
2 L	10	105·95	41·4	41·4	—	—
3 L	10	122·10	50·9	50·7	0·2	0·39
Total	30	318·90	122·7	122·0		
Mean	1	106·30	40·90	40·67	0·23	0·57
1 R	10	89·30	38·2	38·5	0·3	0·78
2 R	10	101·85	38·8	39·6	0·8	2·06
3 R	10	105·80	42·7	43·2	0·5	1·17
Total	30	296·95	119·70	121·30		
Mean	1	98·98	39·90	40·43	0·53	1·33

It is evident from Table 5 that the leaves of the left-spiralled palms produce a small excess of leaflets on the left half, and those of right-spiralled palms produce 1·33 per cent extra leaflets on the right half. However, the difference is far from being significant statistically.

6. **Phoenix sylvestris** Roxb.

Phoenix sylvestris, true to its popular name, wild date, grows in a wild state particularly in the sub-Himalayan belt of India and extending downward to Andhra Pradesh.

Determining the leaf spirals is relatively difficult with *Phoenix sylvestris* on account of the numerous leaves in the crown and because of the conspicuous genetic spirals running opposite to the normal spirals. In a right-spiralled palm, the bunch hangs on the right side of the subtending leaf stalk, and vice versa in a left-spiralled palm. In a leaf of a right-spiralled palm, generally the leaflets on the right half begin to develop from a position lower than the other half, but it is not universal. Mirror image situation is the case with a leaf of a left-spiralled palm (Fig. 2).

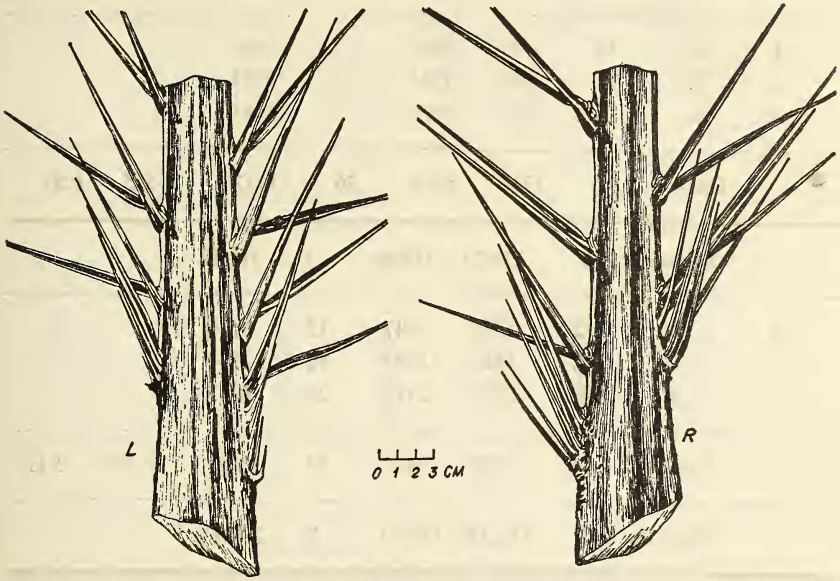

FIG. 2. Dorsal view of portions of leaves from left- and right -spiralled *Phoenix sylvestris*.

Six palms (3 left-spiralled and 3 right-spiralled ones) between 20 and 50 years, growing at the premises of the Indian Statistical Institute, Calcutta, were selected, and 12 leaves from each (20 leaves from tree No. 6) were cut, and measurements and counts made. Data obtained from them are presented in Table 6.

Of the 36 leaves of the left-spiralled palms, two had equal numbers of leaflets on both the halves and in a further 8, the right-half possessed excess leaflets. The excess leaflets on the left half in the remaining 26 leaves ranged from 1 to 8. On the aggregate, a leaf of the left-spiralled palm bore 1·50 per cent more leaflets. Of the 44 leaves from the right-spiralled palms, 3 leaves had the same number of leaflets on both the halves, and in another 6, the left half had extra leaflets. It may be mentioned that all the ' aberrant ' leaves were from a single tree (No. 4) and for this tree the left half produced on an average more leaflets than

the right. In the remaining leaves, the extra number of leaflets per leaf ranged from 1-11. Ignoring tree No. 4 with negative values, it is found

TABLE 6

Phoenix sylvestris: NO. OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED PALMS

Palm	Spiral	No. of leaves	Leaflets on halves		Central leaflet	Total	Variance of (L-R)	% difference
			Left	Right				
1	L	12	1914	1868	12	3794		
2	L	12	1996	1985	12	3993		
3	L	12	1823	1795	12	3630		
	Total	36	5733	5648	36	11417	8·565	1·50
	Mean per leaf		159·25	156·89	1	317·14		
4	R	12	1751	1747	12	3510		
5	R	12	1525	1593	12	3130		
6	R	20	2987	3118	20	6125		
	Total	44	6263	6458	44	12765	13·040	3·11
	Mean per leaf		142·34	146·77	1	290·11		

that the leaves of right-spiralled palms bore on their right half 3·11 per cent more than the left half.

7. **Ptychosperma macarthurii** H. Wendl.

Ptychosperma macarthurii resembles *Chrysalidocarpus lutescens* in producing suckers, bearing a smaller crown and possessing smaller numbers of leaves and leaflets per leaf. Two fruit-bearing shoots each of six clumps were selected, of which one was left-spiralled and the other right-spiralled. All mature leaves from each shoot were cut and measurements and counts taken on them. The number of fully opened green leaves available per shoot ranged from 6-9. The data on the 12 shoots are presented in Table 7.

TABLE 7

Ptychosperma macarthurii: NO. OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED SHOOTS

Clump	Shoot	Spiral	No. of leaves	Leaflets on halves		Total	Variance of (L-R)
				Left	Right		
I	1	L	7	181	174	355	
II	1	L	7	181	170	351	
III	1	L	8	224	204	428	
IV	1	L	6	166	150	316	
V	1	L	6	143	132	275	
VI	1	L	8	216	191	407	
		Total	42	1111	1021	2132	1·99
		Mean per leaf		26·45	24·31	50·76	
I	2	R	7	181	199	380	
II	2	R	7	165	170	335	
III	2	R	8	213	242	455	
IV	2	R	7	174	189	363	
V	2	R	8	192	204	396	
VI	2	R	9	198	212	410	
		Total	46	1123	1216	2339	2·19
		Mean per leaf		24·41	26·44	50·85	

Of the 42 leaves examined from 6 left-spiralled palms, 3 had equal numbers of leaflets on both the halves and in another, the right half had excess leaflets. In the remaining leaves, the excess leaflets on the left half ranged from 1-5. On the aggregate, a leaf of the left-spiralled palm bore 8·81 per cent more leaflets on the left-half. Of the 46 leaves from the 6 right-spiralled palms, 5 leaves bore equal numbers of leaflets on both the halves and in 2 others, the left half bore one leaflet more. The excess leaflets ranged from 1 to 5 per leaf. On the whole, a leaf of the right-spiralled palm bore 8·28 per cent more leaflets on the right half. A leaf of a bearing shoot of *Ptychosperma macarthurii* bears 50 to 80 leaflets on both the halves.

8. **Roystonea regia** (H.B.K.) Cook.

Roystonea regia, popularly known as the Royal Palm, or Bottle palm on account of the peculiar bottle-like appearance of the trunk is very popular in Calcutta. The crown of a mature palm bears about 17

green leaves, and with some difficulty it may be possible to follow the normal leaf spirals. Portions of leaves from the two kinds of palms are shown in Fig. 3. Six leaves each from six palms were collected. Of these

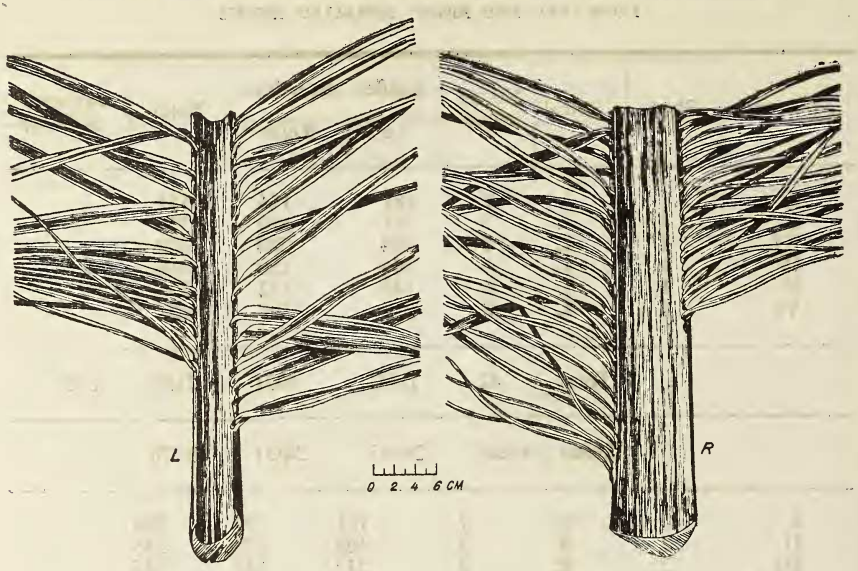

FIG. 3. Dorsal view of portions of leaves from left- and right- spiralled *Roystonea regia*.

4 had left-handed foliar spiral and the others, right-handed spiral. The data are presented in Table 8.

TABLE 8

Roystonea regia: NUMBER OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- HANDED PALMS

Palm	Spiral	Number of leaves	Leaflets on halves		Total	Variance of (L-R)
			Left	Right		
1	L	6	803	760	1563	
2	L	6	855	830	1685	
3	L	6	1315	1290	2605	
4	L	6	1198	1173	2371	
	Total	24	4171	4053	8224	6·06
	Mean per leaf		173·79	168·88	342·67	
5	R	6	1284	1321	2605	
6	R	6	1184	1217	2401	
	Total	12	2468	2538	5006	11·18
	Mean per leaf		205·66	211·50	417·17	

All the 24 leaves of the four left-spiralled palms bore extra leaflets on their left half, the excess leaflets varying from 1-12 per leaf. The overall excess leaflets on the left half over the right was 2·91 per cent.

Among the 12 leaves from the two right-spiralled palms, only one had an extra leaflet on the left half, and in the rest, the excess leaflets on the right half ranged from 2-12 per leaf. The overall excess on the right half in a leaf was 2·84 per cent. All the leaflets remained free like those of the coconut.

B. Palmate palms

Among the five species of palms with palmate leaves studied, *Licuala spinosa* and *Rhapis excelsa* are suckering species. While the very useful *Borassus flabellifer* grows wild in West Bengal as well as in most other regions in India, the other four species are grown in parks and near houses as ornamentals.

9. **Borassus flabellifer** Linn.

In this species, the leaves are arranged in three clear spirals, all running either clockwisely or counter-clockwisely in a palm. The leaves are costa-pinnate and most of them paripinnate. In some leaves, it is rather difficult to make out whether the leaf ends in a pair of leaflets or a single one. Since the mid-ribs of leaflets always appear to fork away from the rachis, the uppermost two leaflets appear as though each belongs to a different half of the lamina, and hence the leaf may be regarded as paripinnate so far as the accounting of the leaflets is concerned.

12 leaves each from 6 palms (3 left-spiralled and 3 right-spiralled) were cut, and counts and measurements made on them. The data are presented in Table 9.

TABLE 9

Borassus flabellifer: NUMBER OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT-HANDED PALMS

Palm	Spiral	Number of leaves	Leaflets on halves		Total	Variance of (L-R)
			Left	Right		
1	L	12	444	443	887	
2	L	12	420	419	839	
3	L	12	510	503	1013	
	Total	36	1374	1365	2739	0·80
	Mean per leaf		38·17	37·92	76·09	
4	R	12	461	464	925	
5	R	12	509	506	1015	
6	R	12	561	547	1108	
	Total	36	1531	1517	3048	1.76
	Mean per leaf		42·53	42·14	84·67	

Of the 36 leaves from the left-spiralled palms, 14 had equal numbers of leaflets on halves, and in 6 others, the right-half had more leaflets. In the remaining 16 leaves, the excess leaflets on the left-half was only one per leaf excepting an odd case where the difference was two. The percentage excess of leaflets on the left half over the right is 0.66%. Among the 36 leaves from the right-spiralled palms, 5 leaves had the same number of leaflets on both the halves, and in a further 19, the left half bore more leaflets. The percentage excess on the right half is in the negative, reaching – 0·92%. Thus, in this species the left half of leaves from both the types of palms possessed a small excess number of leaflets, although the difference is not statistically significant.

10. **Licuala spinosa** Wurmb.

As its name suggests, *Licuala spinosa* is beset with numerous prominent spines on the long and slender petioles on either margin, and many suckers at various ages spring from the same clump. Observations were made on a single clump growing at the Indian Statistical Institute having over 40 suckers. Shoots bearing over three metres of stem and bearing flower bunches only were cut and their leaves examined. Only five left-handed and 6 right-handed shoots were available for observation. Portions of the two kinds of leaves are shown in Fig. 4. The data collected on these 11 shoots are presented in Table 10.

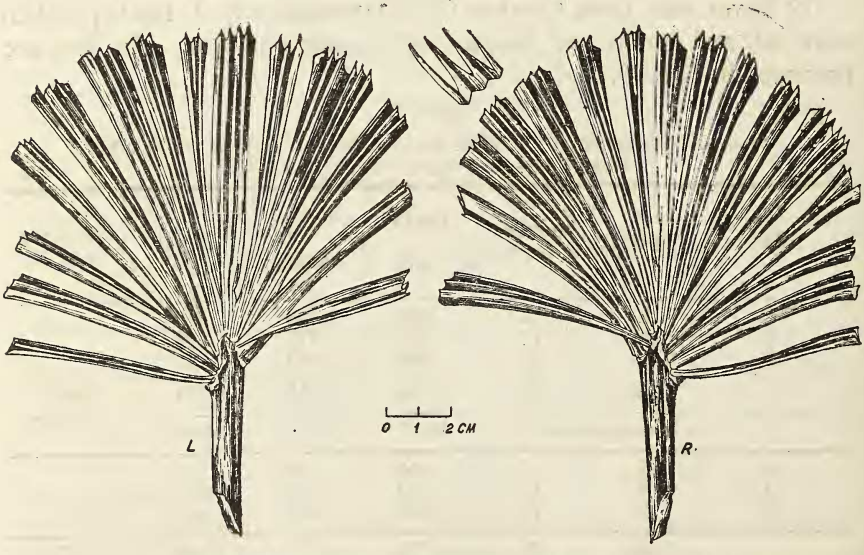

FIG. 4. Dorsal view of portions of leaves from left- and right- spiralled *Licuala spinosa*.

TABLE 10

Licuala spinosa : NO. OF LEAFLETS ON HALVES FROM LEFT- AND RIGHT- SPIRALLED SHOOTS

Shoot	Spiral	No. of leaves	Leaflets on halves		Central	Total	Variance of (L-R)
			Left	Right			
1	L	9	216	207	56	479	
2	L	8	180	169	48	397	
3	L	8	193	187	46	426	
4	L	6	137	123	37	297	
5	L	16	374	337	119	830	
	Total	47	1100	1023	306	2429	2·40
	Mean per leaf		23·40	21·77	6·51	51·68	
6	R	14	361	371	81	813	
7	R	11	270	286	61	617	
8	R	6	143	145	31	319	
9	R	7	171	172	34	377	
10	R	5	117	118	25	260	
11	R	5	115	117	26	258	
	Total	48	1177	1209	258	2644	1·51
	Mean per leaf		24·52	25·19	5·37	55·08	

In a left-spiralled palm, usually the leaflets on the right half are seen developing from below those on the other half, and vice versa in a right-spiralled palm. Among the 47 leaves from 5 left-handed shoots, the number of leaflets on both the halves was the same in 10, and only in 2 others, the leaflets on the right half were in excess. On the whole, a leaf of a left-spiralled palm produced 2·72 extra leaflets on the left half than on the right. However, a minor deviation was followed with this species. The leaf is costa-pinnate and the leaflets remain fused in twos, threes, fours and even fives. Only a little over one per cent of the leaflets are, however, free. A few leaflets remain fused at the tip of the compressed peduncle and this cluster is regarded as the odd group and ignored for estimating the number of leaflets on the halves. The central cluster is composed of 4-9 leaflets, which is about 11% of the total leaflets. In the left-spiralled palms, the mean figure for the central leaflets (6·51) was slightly in excess of that for the right-spiralled palms (5·37).

Of the 48 leaves of the six right-spiralled palms, 18 had equal numbers of leaflets on the halves and in a further 5, the left half had more leaflets. However, on the aggregate, the right half of a right-spiralled leaf bore 2·73 per cent excess leaflets.

11. Livistona chinensis R. Br.

Livistona chinensis with its luxuriant green crown bearing about 50 green leaves flourishes in Calcutta. Since the stalk of the fruiting bunch is quite long, it clearly slants either to the left of the subtending leaf or to its right. In a left-spiralled palm, the bunch leans (or hangs) on the left side of the subtending leaf, and vice versa, in a right-hander. Leaves from left-spiralled and right-spiralled palms are seen in Fig. 5. Twelve

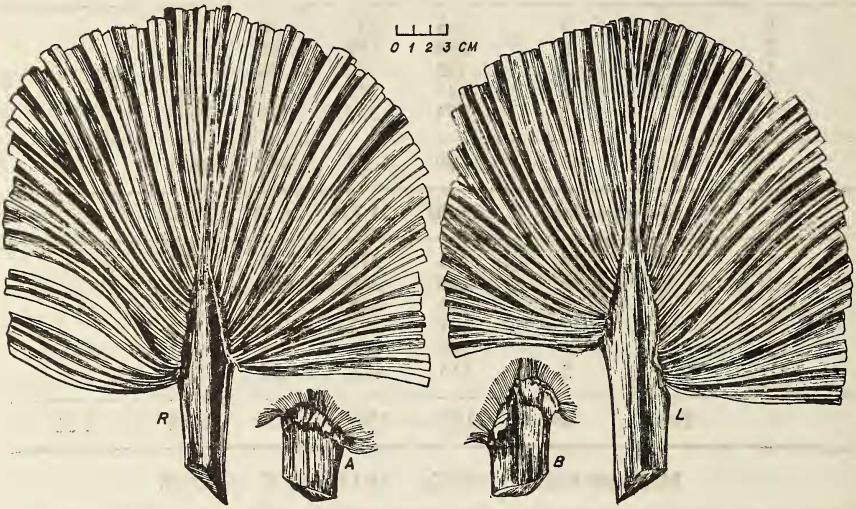

FIG. 5. Ventral view of portions of leaves from right- and left- spiralled *Livistona chinensis*.
Inserts *A* and *B* show the comb on the dorsal side of the lamina-base in these leaves.

leaves each of the 6 palms were harvested and measurements and counts made on them. Data on the left-and right-spiralled palms are presented in Table 11.

TABLE 11

Livistona chinensis: NO. OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED PALMS

Palm	Spiral	No. of leaves	Leaflets on halves		Total	Variance of (L-R)
			Left	Right		
1	L	12	524	520	1044	
2	L	12	546	541	1087	
3	L	12	568	574	1142	
	Total	36	1638	1635	3273	0·69
	Mean per leaf		45·50	45·42	90·92	
4	R	12	545	555	1100	
5	R	12	500	497	997	
6	R	12	537	540	1077	
	Total	36	1582	1592	3174	2·36
	Mean per leaf		43·94	44·22	88·16	

Of the 36 leaves from the left-spiralled palms, 9 had equal numbers of leaflets on both the halves and in a further 13, the left half had more leaflets. The difference in the rest of the leaves between halves was not appreciable and the number of leaflets on both the halves of many leaves was almost similar. The percentage difference between halves was only 0·18. Among the 36 leaves of the right-spiralled palms, in 13, the number of leaflets on both the halves were similar, and in a further 10, the leaflets on the left half were slightly in excess of those in the right half. The overall picture did not show that the right half has significantly more leaflets than the left, the percentage difference being only 0·63.

Though the leaf of *L. chinensis* is also costa-pinnate, the tip of the rachis can be hardly made out, and the last leaflet may be regarded as deviating either to the left half or the right. Thus, there is no terminal odd leaflet as in *Phoenix sylvestris* or a cluster of leaflets as in *Licuala spinosa*.

12. **Livistona rotundifolia** Mart.

The adult *Livistona rotundifolia* palm is much taller than *L. chinensis* and the former flowers once every year in February-April in Calcutta. It has fewer leaves than the latter. The data are presented in Table 12.

TABLE 12

Livistona rotundifolia: NO. OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED PALMS

Palm	Spiral	No. of leaves	Leaflets on halves		Central	Total	Variance of (L-R)
			Left	Right			
1	L	12	573	575	12	1160	
2	L	11	513	506	6	1025	
3	L	12	505	505	11	1021	
Total		35	1591	1586	29	3206	3·89
Mean per leaf			45·46	45·31	0·83	91·60	
4	R	12	568	571	2	1141	
5	R	12	493	498	8	999	
6	R	12	489	500	10	999	
Total		36	1550	1569	20	3139	2·58
Mean per leaf			43·06	43·58	0·56	87·20	

Of the 35 leaves from the left-spiralled palms, 8 had the same number of leaflets on both the halves. In a further 12 leaves, the right half bore more leaflets. On the aggregate, the difference between the two halves was not significant. The left half bore only 0·32 per cent excess leaflets. As seen from Table 12, one tree on an average produced more leaflets on the right half of its leaves and another had equal numbers of leaflets on both the halves.

Of the 36 leaves from the right-spiralled trees, 6 leaves had equal number of leaflets on both the halves and in another 12, the left half had excess leaflets. In spite of these deviations, each tree produced a small extra number of leaflets on the right half. However, the difference in no tree was statistically significant. The overall percentage difference between the two halves is 1·23.

Unlike *L. chinensis*, many leaves of *L. rotundifolia* are imparipinnate and the odd leaflet was difficult to be grouped with any side. However, it is not universal with all the leaves. Tree 1 had all the leaves ending with an odd terminal leaflet while only 2 out of 12 leaves of tree 4 had odd leaflets. Sixty per cent of the leaves from all the 6 palms were imparipinnate.

13. **Rhapis excelsa** Bl.

The rattan, *Rhapis excelsa* in India is an ornamental palm although occasionally its stem is used as a walking stick. In young palms the lamina is bilobed and resembles a pinnate leaf. The number of leaflets that form one of the lobes is significantly more than that on the other

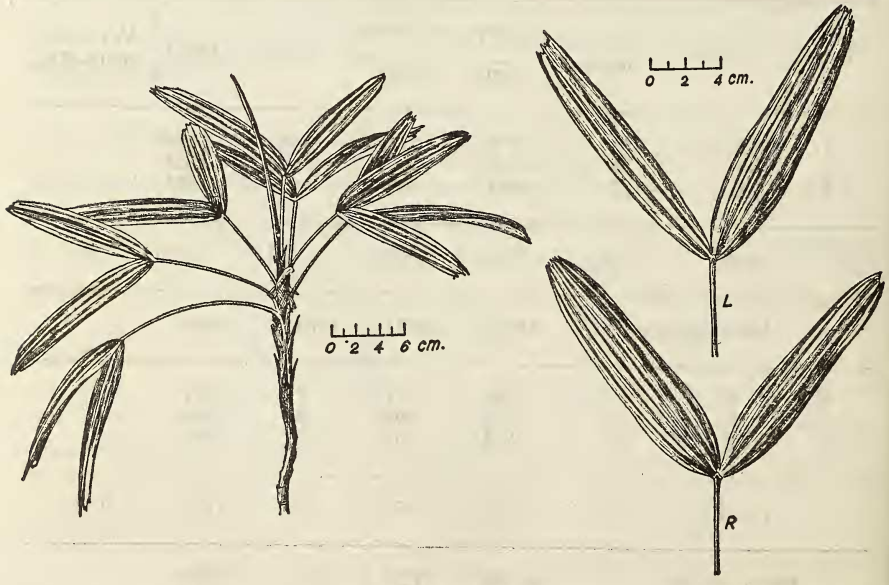

FIG. 6. A shoot of young *Rhapis excelsa*. *L* and *R* are dorsal view of leaves from left-spiralled and right-spiralled palms.

lobe. In a left-spiralled palm the left half possesses significantly more leaflets than its right half, and vice versa, for a leaf of a right-spiralled palm. In Fig. 6 is seen a shoot of a young *Rhapis* palm and dorsal view of one leaf each from left-spiralled and right-spiralled palms.

45 leaves from 6 left-spiralled shoots and 34 leaves from 5 right-spiralled leaves were examined for the number of leaflets, and the data presented in Table 13.

TABLE 13

Rhapis excelsa : NUMBER OF LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED PALMS

Palm	Spiral	No. of leaves	Length of lamina (cm.)	Leaflets on halves			Variance
				Left	Right	Total	
1	L	10	215·0	67	56	123	
2	L	6	117·5	36	26	62	
3	L	8	131·0	51	40	91	
4	L	7	108·3	38	28	66	
5	L	8	139·3	57	42	99	
6	L	6	94·0	36	28	64	
Total		45	805.1	285	220	505	4·3
Mean per leaf			17·89	6·33	4·89	11·22	
1	R	6	79·0	24	36	60	
2	R	8	131·0	41	56	97	
3	R	5	99·5	25	35	60	
4	R	6	136·5	31	42	73	
5	R	9	156·5	42	59	101	
Total		34	602·5	163	228	391	7·04
Mean per leaf			17·72	4·79	6·70	11·50	

The left lobe of all the leaves from all the left-spiralled plants had excess leaflets compared to their corresponding right half. Similarly without any exception the right lobe of all the leaves from right spiralled plants bore extra leaflets. The percentage difference between halves of leaves of the left-spiralled shoots was 29·54 per cent and the corresponding figure for the right-spiralled ones was 39·88. *Rhapis excelsa* had shown the maximum value for the difference among all the species studied so far.

C. Palms with bipinnate leaves

The species, *Caryota mitis*, is much smaller than *C. urens*, and the former is a suckering species while the latter is single-stemmed. Both are monocarpic palms which complete their life after the first flush of flowering as the main stem ends in an inflorescence.

14. **Caryota mitis** Lour.

Within a clump, left- and right- spiralled shoots are generally noticeable. A shoot at the flowering stage may produce a trunk of 2-4 metres high. The leaves are bipinnate. Usually the distal 2-4 secondary rachises are unbranched. The lamina of a mature leaf measures a little less than 3 metres. The main rachis is paripinnate, but almost all secondary rachises are imparipinnate. Portions of two leaves are shown in Fig. 7.

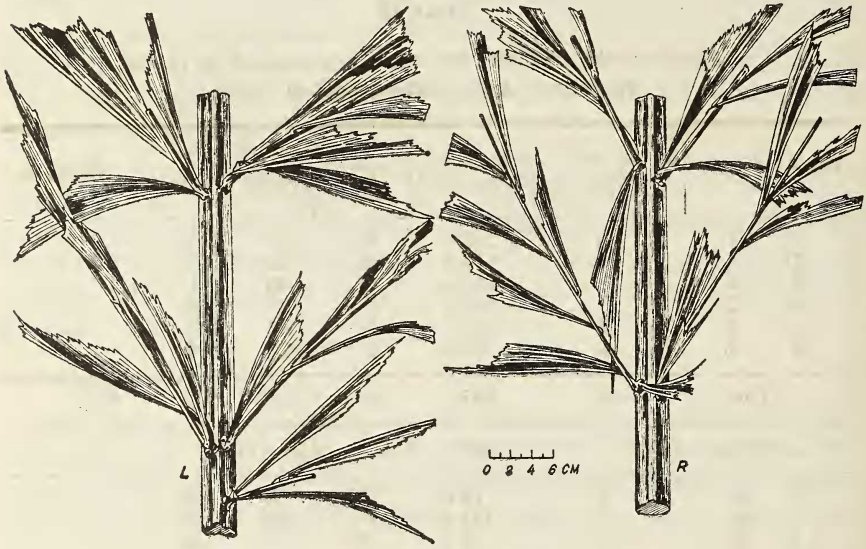

FIG. 7. Dorsal view of portions of leaves from left- and right- spiralled *Caryota mitis*.

Twelve leaves from three left-spiralled palms and 11 from three right-spiralled palms were examined at the Indian Botanic Garden, Calcutta. The secondary branches/leaflets and the leaflets on the secondary as well as primary rachises were counted separately for each half and the data on 23 leaves are given in Table 14.

The general trend that a left-spiralled palm produces an excess of leaflets on the left half of the leaf (compared to the right) is indicated in the present case also since the left half bore 1·98% more leaflets. The reverse situation with a leaf of a right-spiralled shoot is also apparent. Here the right half bore more leaflets than the left half, and the difference was 2·24 per cent. It is also clear from Table 14 that the number of rachises on a particular half increases if it bears a greater number of leaflets.

Each secondary rachis bears one odd leaflet at its tip and two rows of leaflets spread along the same plane of the main rachis (also that of the secondary rachises). Hence some leaflets are distributed with their

tips pointing towards the distal end of the leaf, while the others pointing towards the base of the leaf. These leaflets were separately accounted

TABLE 14

Caryota mitis : NO. OF LATERAL RACHISES (LEAFLETS) ON HALVES OF LEAVES FROM LEFT- AND RIGHT- SPIRALLED PALMS

Shoot	Spiral	No. of leaves	Lateral rachises/leaflets on halves Left		Right		Total	
			Rachi-ses	Leaf-lets	Rachi-ses	Leaf-lets	Rachi-ses	Leaf-lets
1	L	6	95	1508	92	1476	187	2984
2	L	5	56	643	56	637	112	1280
3	L	1	14	222	14	214	28	436
	Total	12	165	2373	162	2327	327	4700
	Mean per leaf		13·75	197·75	13·50	193·92	27·25	391·67
1	R	5	58	998	61	1023	119	2021
2	R	5	69	1106	70	1126	139	2232
3	R	1	14	216	15	223	29	439
	Total	11	141	2320	146	2372	287	4692
	Mean per leaf		12·82	210·91	13·27	215·64	26·09	426·55

for with the leaves of two shoots. A greater number of leaflets are produced on the side of the lateral rachises facing the stalk than those pointing to the distal end.

A secondary rachis with the leaflets it bears is morphologically similar to a leaflet in other species of palms (Periasamy 1962, 1966a & b). In an embryonic palm leaf, two main regions are perceivable—the main body (which develops into the leaf sheath, the petiole and the main rachis), and the lamina wing which develops into leaflets including the secondary rachises in *Caryota* sp.

15. **Caryota urens** Linn.

Eighteen leaves each from 4 right-spiralled and 9 leaves from three left-spiralled *Caryota urens* palms were examined. The lamina region of *C. urens* is much larger than that of *C. mitis* although this varies greatly with individuals. Lower portions of two leaves from right-spiralled

and left-spiralled palms are seen in Fig. 8. The number of secondary rachises for each leaf and the number of leaflets in each secondary

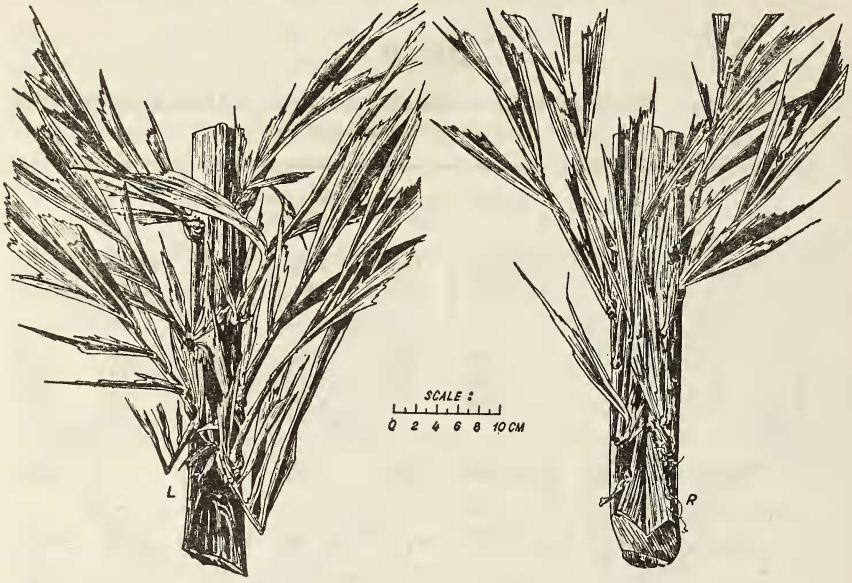

FIG. 8. Dorsal view of portions of leaves from left- and right-spiralled *Caryota urens*.

rachis as well as the main rachis were accounted for separately. The data are presented in Table 15.

TABLE 15

Caryota urens : NO. OF LATERAL RACHISES/LEAFLETS ON HALVES OF LEAVES FROM LEFT- AND RIGHT-SPIRALLED PALMS

Palm	Spiral	No. of leaves	Lateral rachises & Leaflets on halves				Total	
			Left		Right		Rachises	Leaflets
			Rachises	Leaflets	Rachises	Leaflets		
1	L	3	72	1845	70	1823	142	3668
2	L	3	72	2165	72	2185	144	4350
3	L	3	71	1957	70	2040	141	3997
Total		9	215	5967	212	6048	427	12015
Mean per leaf			23.89	663.00	23.56	672.00	47.45	1335.00
1	R	3	58	1772	61	1911	119	3683
2	R	3	70	1930	70	1834	140	3764
3	R	6	123	2567	127	2615	250	5182
4	R	6	108	2762	114	2806	222	5568
Total		18	359	9031	372	9166	731	18197
Mean per leaf			19·94	501·72	20·67	509·22	40·61	1010·94

* A leaf of the left-spiralled palm bore on an average 47·44 secondary rachises and 1335·00 leaflets. Out of the nine leaves, only two had extra secondary rachises on the left half and all did not bear extra leaflets on this left half. But the right half bore, on an average, 1·36 per cent more leaflets than the left half.

From observations made on the 18 leaves of the right-spiralled palms, it was found that a leaf on an average bore 40·61 secondary rachises and 1010.90 leaflets. The right half of a leaf of a right-spiralled palm bore a slight excess of secondary rachises as well as leaflets. The percentage excess of leaflets on the right-half over the left accounted for only 1·49 per cent.

Discussion

The leaves of all types of palms are practically asymmetric bilaterally as evidenced by the data on the number of leaflets presented in the preceding tables. This asymmetry is caused primarily by the spiral arrangement of leaves on the trunk. From a study on the arrangement of leaves in a number of palm species, Davis (1970c) had generalised that any two consecutive leaves on a palm are placed at an angle of 137·5°. This angular deflection makes with the remaining angle (222·5°) to complete one full revolution, a proportion, 0·618 which is spoken of as Golden Proportion.

In some species of palms like *Areca catechu*, only a single foliar spiral is visible. But in *Arenga pinnata* two spirals are clearly visible. Palms like *Borassus flabellifer* possess three distinct spirals. *Cocos nucifera* bears five and *Elaeis guineensis* eight clear spirals. From the scars of *Phoenix canariensis*, thirteen spirals can often be made out. All the above numbers (1, 2, 3, 5, 8, 13) happen to be the stages in the Fibonacci Sequence. That a palm gets a foliar number synchronising with one of the Fibonacci Numbers has been attributed to the fact that the leaves are arranged according to the Golden Proportion. The Fibonacci Numbers, excepting the few lower ones, also make the same ratio between consecutive ones. One point arising from the number of spirals per tree has been given adequate consideration. All species of palms which show only one spiral each will fall in conformity with the spiral formed on the basis of two consecutive leaves from the direction of the older towards the younger leaf. But in a palm having two clear spirals, the direction of the spirals will be opposite to the single spiral. The direction of the spirals of palms showing three or eight spirals is like that of the single spiral. But the two, five as well as the thirteen spirals run opposite to the single spiral. It may be remembered that the numbers 1, 3, 8 etc. alternate with 2, 5, 13 etc. in the Fibonacci Sequence. Therefore, the apparently visible foliar spirals in some species of palms do not synchronise with the direction of the single spiral based on the position of two consecutive leaves. Therefore, the direction of the single spiral was followed for all the species.

The pinnate leaves show bilateral asymmetry more vividly than the palmate and bipinnate types. However, young *Rhapis excelsa* of

the palmate type is an exception. Although all *R. excelsa* palms later on develop palmate leaves, young seedlings with their two undivided halves appear more pinnate.

In *Caryota* sp., the secondary rachises which correspond to the leaflets in other species do not show any significant difference in their numbers between halves although the difference is in the expected direction. However, the number of the ultimate leaflets happen to be slightly more on the right half of leaves belonging to the left- as well as the right-spiralled palms. But the difference is very small.

A mention may be made in favour of Corner (1966) who described the *Caryota* as having imparipinnate main rachis, which was criticized by Moore Jr. (1967). But the main rachis in 34·62% of the leaves of *Caryota urens* examined by us ended in a single leaflet. Of the 1158 secondary rachises relating to the 27 leaves, 8·64% deviated from the general rule by having a pair of leaflets at their tip (instead of a single leaflet). It would appear, therefore, that Moore's criticism on this point is not based on the whole truth.

In order to find out the possible factors influencing the asymmetry, the number of green leaves a palm bears at a time, number of leaflets per leaf, length and area of the lamina, thickness of the stem, and the number of foliar spirals per species were considered. Of these, the number of green leaves per crown seems to have a positive association on the asymmetry of the lamina. Table 16 gives the mean number of leaves per species and the percentage difference in the number of leaflets between halves of leaves for 15 species. In some of them the percentage difference relating to the leaves of left-spiralled palms differed greatly from those of the right-spiralled ones as in *Rhapis excelsa*. Hence, the mean of the two percentages was worked out and the values given under the last column of Table 16.

When the above data are plotted (Fig. 9), the species with pinnate leaves (young palms of *Rhapis excelsa* are regarded as pinnate) show a greater degree of association between the number and the asymmetric nature of the leaves. The palmate species occupy the lower position in the graph. The two species having bipinnate leaves fall between the pinnate and palmate types. *Phoenix sylvestris* having about eighty green leaves and showing an appreciable difference between halves of leaves finds its position very odd. The data on *Nypa fruticans* are too limited to attach importance on their significance.

Species having smaller numbers of green leaves per crown show the difference between halves more conspicuously than those with larger number of leaves.

One of the reasons for this situation seems to be that with fewer leaves in the crown, they undergo a greater torsion to cope up with the

wider space available than a species having a greater number of leaves in the crown. In the latter case, the leaves making very narrow internodes on relatively thick stems seem to show the least torsion and thus

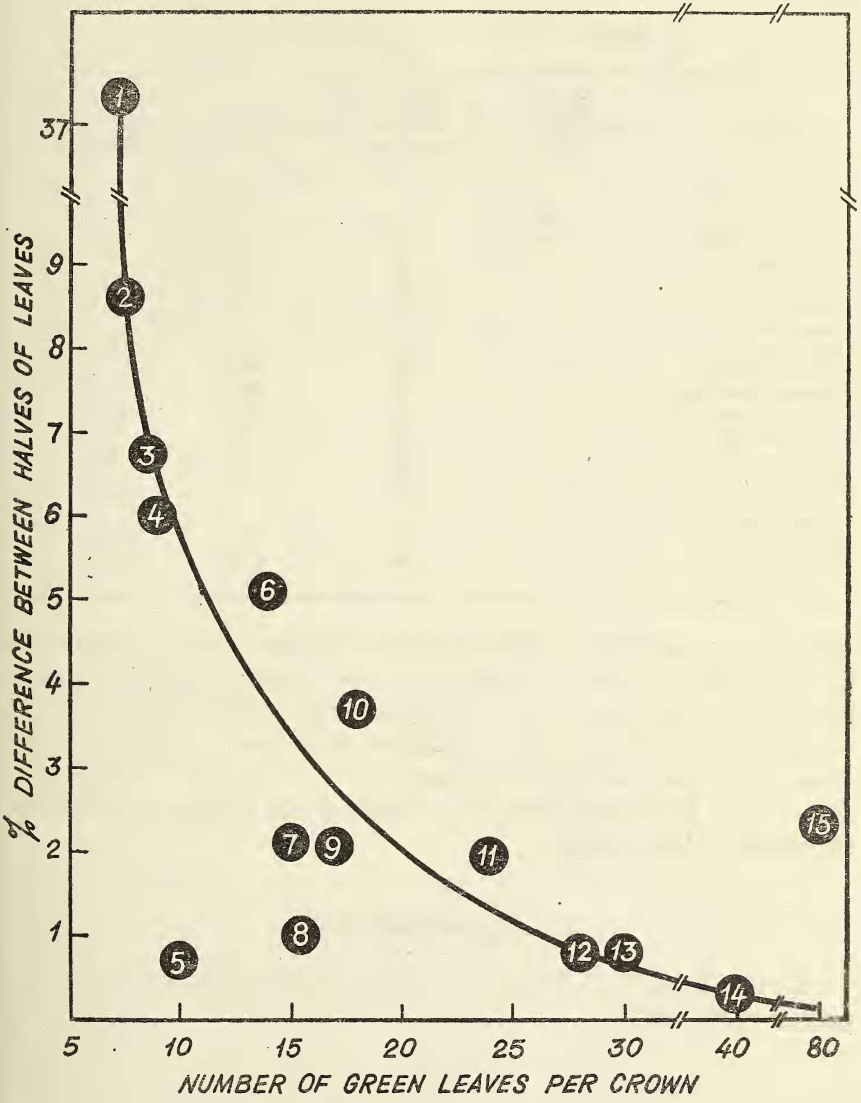

FIG. 9. Graph showing the percentage difference in the number of leaflets between halves of leaves.

The numbers represent: 1. *Rhapis excelsa*; 2. *Ptychosperma macarthurii*; 3. *Areca catechu*; 4. *Chrysalidocarpus lutescens*; 5. *Nypa fruticans*; 6. *Licuala spinosa*; 7. *Caryota mitis*; 8. *Phoenix paludosa*; 9. *Roystonea regia*; 10. *Caryota urens*; 11. *Cocos nucifera*; 12. *Livistona rotundifolia*; 13. *Borassus flabellifer*; 14. *Livistona chinensis*; 15. *Phoenix sylvestris*.

unfold along the same direction of their origin. The structure of the stem also supports this view. A striking analogy is the situation met

TABLE 16

SUMMARY OF DATA ON 15 SPECIES OF PALMS

Species	No. of experimental palms	No. of leaves examined	No. of green leaves per palm	% diff. between halves of leaves
Areca catechu	6	47	8·5	6·78
Borassus flabellifer	6	72	30·0	0·72
Caryota mitis	6	23	15·0	2·11
Caryota urens	7	27	18·0	1·44
Chrysalidocarpus lutescens	12	88	9·0	6·04
Cocos nucifera	6	72	24·0	1·93
Licuala spinosa	11	95	14·0	5·11
Livistona chinensis	6	72	40·0	0·41
Livistona rotundifolia	6	1	28·0	0·77
Nypa fruticans	1	10	10·0	0·90
Phoenix paludosa	6	60	15·5	0·96
Phoenix sylvestris	6	80	80·0	2·31
Ptychosperma macarthurii	12	88	7·5	8·56
Rhapis excelsa	11	79	7·2	33·94
Roystonea regia	6	36	17·0	2·88

with in *Agave sisalana.* The leaves of young agave plants having three or four leaves are greatly asymmetric. The numbers of spines on both the margins are unequal. In a left-spiralled plant the left margin bears a significantly greater number of spines, when young. But when the plants grow and possess 40-50 green leaves, the leaves become more symmetric. That is, the numbers of spines on the margins do not differ significantly (Mitra 1968).

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